

SHORT COMMUNICATIONS

Temporal stability of song in a local population of Wood Thrushes.—In many species of songbirds, individuals acquire song through social learning (see review by Slater 1989). As a result, song is subject to cultural evolution. Inferences about the process of cultural evolution can be made from an analysis of geographical variation in song, and a number of studies has taken this approach (see, e.g., Lynch et al. 1989 and references therein). A second approach, more direct than the first but also more time-consuming, is to examine temporal changes in song within a population (e.g., Thompson 1970, Jenkins 1978, Ince et al. 1980, Payne et al. 1981, McGregor and Krebs 1982, Payne 1985, Gibbs 1990).

Here I examine temporal variation within a population of Wood Thrushes (*Hylocichla mustelina*). An earlier longitudinal study which compared samples of Wood Thrush song recorded 14 years apart in Sapsucker Woods, Ithaca, New York, revealed no significant differences between the samples (Whitney and Miller 1987a). That study, however, was based on small sample sizes, and my objective here is to present more detailed and compelling evidence for a lack of temporal change in Wood Thrush song.

Materials and methods.—I compared two samples of song recorded from Wood Thrushes living on and near the grounds of the Rockefeller University Field Research Center, Millbrook, New York (see fig. 2 of Whitney and Miller 1987a). One sample was recorded in 1981 (8 May–4 June) and the second in 1990 (6–9 June) ($N = 36$ and 26 birds, respectively). Copies of these recordings are available from the author.

A typical Wood Thrush song has three phrases, referred to as the A, B, and C phrases (for sonagram, see fig. 1 of Whitney and Miller 1987a). The introductory A phrase consists of one or more low-pitched sounds, the middle B phrase is of loud, flute-like notes, and the ending C phrase is usually a trill. My analysis is based on the structure of the B phrase, which is the only part of the song that appears to be learned by imitation (Lanyon 1979, Whitney and Miller 1987b). Individual males have repertoires of two to eight different B phrases.

In both years, I attempted to record a sequence of at least 30 songs from each bird. This seemed adequate to identify the complete B phrase repertoire, since Wood Thrushes typically cycle through their repertoires in sequences of 15 songs or fewer. Recordings were made with a Uher Report IC tape recorder equipped with either a Sennheiser MKH 815T directional microphone or a Dan Gibson P650 parabolic microphone and a Sony TC-D5M cassette recorder equipped with either a Dan Gibson P650 or a Sony PBR-330 parabola and Sony ECM-170 microphone.

Sonagrams were prepared with a Macintosh Plus computer, a MacADIOS 411 hardware unit, a TTE 411AFS amplifier and anti-aliasing system, and MacSpeech Lab software (GW Instruments). The recording sample rate of the system was set at 10.416 kHz (according to which rate the maximum frequency displayed on a sonagram is 5 kHz), and the wide band filter (300 Hz) was used. I measured durations of song parameters from wide band sonagrams and dominant frequencies from narrow band (45 Hz filter) "spectrum" waveforms.

Results.—The system of song classification used in this study was described in detail in an earlier paper (Whitney and Miller 1987a) and is based on the 1981 sample. It placed 141 of the 154 songs (92%) in that sample into 25 discrete structural types (Table 1). Applied to the 1990 sample, the system classified 105 of 114 songs (92%). Twenty-three of the 25 types were represented in the 1990 sample (Table 1).

In the original classification of the 1981 sample (Whitney and Miller 1987a), I required that each defined song type be shared by two or more birds in the sample. Thus, for each

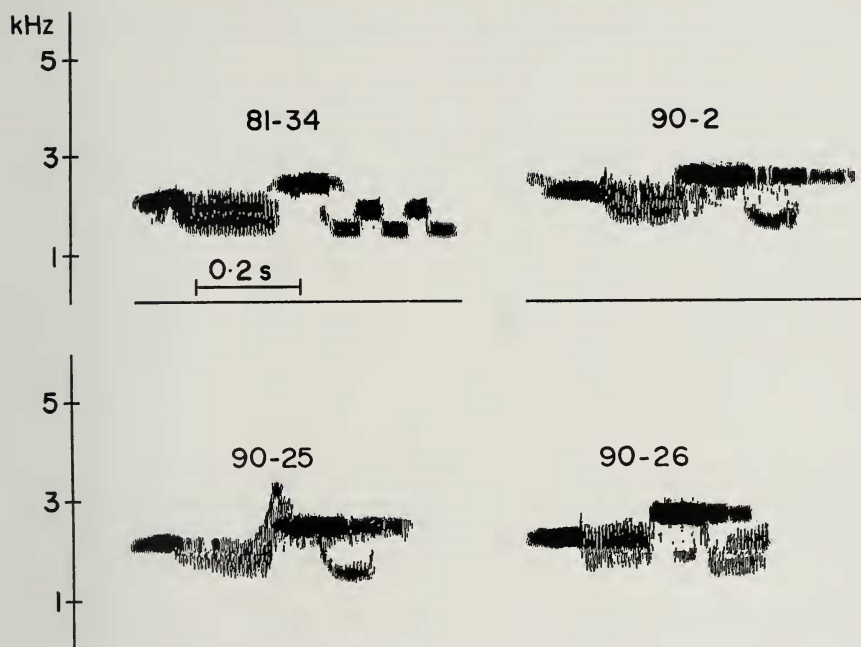


FIG. 1. Type 16 B phrase from 1981 (top left) and three unclassified phrases from 1990.

type there was evidence of learning by imitation. If the same criterion is applied to the 1990 sample, one additional song type must be defined. This type, resembling a variant of Type 16 that lacks a terminal trill, was shared by three birds (Fig. 1).

Superficially, the relative abundances of the different types appear similar for 1981 and 1990 (Table 1). Type 1 was the most common type in both samples, and Types 4, 6, 8, 12, 13, 16, and 23 were among the 10 most common types in both samples. The Spearman rank correlation between the two samples is 0.81 ($P < 0.001$). Despite this significant correlation, the possibility remains that the samples differ subtly. To check for such differences, I used a G -test (Zar 1984) to compare the samples with respect to the abundances of the eight most common (both samples combined) song types. These eight types included all those for which the expected abundances were greater than five. The results indicate no difference between the samples ($G = 7.14$, $df = 7$, $P > 0.25$).

Using multivariate analysis of variance (from the SYSTAT statistical package), I compared the structure of Type 1 B phrases in the two samples. A typical Type 1 phrase consists of a sequence of four unmodulated notes, each sustained on a relatively constant frequency (see fig. 4 of Whitney 1989). The analysis was based on the following seven parameters of Type 1 phrases: (1–3) time from the onset of each of the first three notes to the onset of the following note, and (4–7) dominant frequency of each note, taken 0.05 sec after the onset of the note.

For each of these parameters, the difference between the two years was only slight (Table 2), and the results of the analysis of variance showed no significant difference between the 1981 and 1990 phrases ($F = 0.67$, $df = 7, 27$, $P = 0.70$).

TABLE 1
ABUNDANCES OF SONG TYPES IN THE 1981 AND 1990 SAMPLES

Type	1981		1990	
	Abundance	Percent	Abundance	Percent
1	20	13.0	15	13.2
2	2	1.3	1	0.9
3	3	1.9	1	0.9
4	14	9.1	9	7.9
5	5	3.2	3	2.6
6	6	3.9	4	3.5
7	4	2.6	2	1.8
8	11	7.1	9	7.9
9	3	1.9	0	0.0
10	3	1.9	8	7.0
11	4	2.6	3	2.6
12	7	4.5	9	7.9
13	9	5.8	10	8.8
14	6	3.9	3	2.6
15	2	1.3	1	0.9
16	10	6.5	4	3.5
17	2	1.3	1	0.9
18	3	1.9	2	1.8
19	3	1.9	5	4.4
20	3	1.9	1	0.9
21	5	3.2	2	1.8
22	2	1.3	1	0.9
23	8	5.2	10	8.8
24	3	1.9	1	0.9
25	3	1.9	0	0.0
Unclassified	13	8.4	9	7.9
Total	154	100.0	114	100.0

Discussion.—The results demonstrate a striking similarity of song between the two samples: (1) of 25 song types defined for the 1981 sample, 23 were found in 1990, (2) the relative abundances of the different song types were the same in the two samples, and (3) according to a multivariate analysis of variance, the structure of the most common song type was the same in the two samples. The only discernable difference between the two samples was the presence in 1990 of one song type that was absent in 1981. These results are consistent with those of the earlier longitudinal study (Whitney and Miller 1987a). In that study, 12 of the 13 song types recorded in Sapsucker Woods in 1969 ($N = 11$ birds) were present in 1981 ($N = 16$ birds), together with four new types. The relative abundances of the different types were significantly correlated in the two samples. The results are also consistent with earlier reports of a lack of geographical variation in Wood Thrush song (Whitney and Miller 1987a, Whitney 1989).

Thus, compared with other songbirds that have been studied in detail (see references above), Wood Thrushes appear to have song that is unusually resistant to change. This

TABLE 2
PARAMETER VALUES^a

Parameter	1981 ^b	1990 ^c
Onset of 1st note to onset of 2nd note (s)	0.12 ± 0.004	0.12 ± 0.006
Onset of 2nd note to onset of 3rd note (s)	0.13 ± 0.005	0.12 ± 0.007
Onset of 3rd note to onset of 4th note (s)	0.10 ± 0.007	0.11 ± 0.006
Dominant frequency of 1st note (Hz)	2540 ± 97.5	2500 ± 138.9
Dominant frequency of 2nd note (Hz)	2000 ± 89.3	2050 ± 127.3
Dominant frequency of 3rd note (Hz)	3450 ± 139.6	3400 ± 167.9
Dominant frequency of 4th note (Hz)	2900 ± 122.2	2900 ± 152.5

^a All values are means ± SE.

^b N = 20.

^c N = 15.

resistance evidently does not result from a lack of "mutant" songs as raw material for evolution, since 8% of the songs in each sample were unclassified (Table 1; see also table 1 of Whitney and Miller 1987a). Perhaps, as I have proposed elsewhere (Whitney and Miller 1987a), mutant songs are at a selective disadvantage in the cultural transmission of Wood Thrush song.

This hypothesis can account for the lack of success of mutant songs but not for the apparent stability over a nine-year period in the relative abundances of the 25 defined song types. It seems plausible that a frequency dependent process is responsible for this stability. For example, the probability of a given song type being learned might be inversely related to the relative abundance of that type in the population (Whitney and Miller 1987a). Other frequency-dependent mechanisms are also possible. Reporting on a study of Darwin's Medium Ground Finches (*Geospiza fortis*), Gibbs (1990) proposed that males with rare song types might be more easily recognized by neighbors and thus at an advantage over males with common song types.

An alternative hypothesis invokes dispersal to account for the lack of geographical variation in Wood Thrush song (Whitney 1989). This hypothesis can be applied as follows to the present results: If male Wood Thrushes learn their songs while still in their natal areas, subsequent dispersal would have a retarding effect on temporal change in song. Suppose (in the simplest case) that all songs, including mutant ones, are selectively neutral. Within a local area, some mutant songs would be learned by fledgling males, but the continual turnover of mutant songs would act as a brake on directional evolution of song in the area. The first step in testing this hypothesis should be to evaluate the assumption that male Wood Thrushes learn their songs before dispersal from natal areas. Two points regarding this assumption can be made here: (1) within a local population the degree of song type sharing does not vary as a function of the distance between males, suggesting that little or no learning occurs after males have settled on breeding territories (Whitney and Miller 1987a). The possibility remains that learning occurs after dispersal but before males settle on territories. (2) Captive Wood Thrushes are able to learn B phrase repertoires of normal size and complexity when tutored with recorded song between the ages of 20 and 80 days (Whitney and Miller 1987b). These results are consistent with the assumption, but a critical test will require detailed field studies (see, e.g., Payne et al. 1981).

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Egg destruction by Eastern Meadowlarks.—Destruction of eggs by passerines is a relatively rare phenomenon confined mainly to the Troglodytidae and Mimidae. Egg pecking has been reported for Marsh Wrens (*Cistothorus palustris*; Allen 1914; Verner 1975; Picman 1977a, b; Bump 1986), Sedge Wrens (*C. platensis*; Picman and Picman 1980), House Wrens (*Troglodytes aedon*; Kendeigh 1941, Belles-Isles and Picman 1986a), Bewick's Wrens (*Thryomanes bewickii*; J. Picman, unpubl. data), Cactus Wrens (*Campylorhynchus brunneicapillus*; Anderson and Anderson 1973), Gray Catbirds (*Dumetella carolinensis*; Belles-Isles and Picman 1986b), and four species of Galapagos mockingbirds (*Nesomimus* spp.; Bowman